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REVIEW ARTICLE

Plant coevolution: evidences and new challenges

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Coevolution has been defined as the reciprocal genetic change in interacting species owing to natural selection imposed by each on the other. The process of coevolution between plants and the surrounding biota – including viruses, fungi, bacteria, nematodes, insects, and mammals – is considered by many biologists to have generated much of the earth's biological diversity. While much of the discussion on plant coevolution focuses on single plant–enemy interactions, a wide array of other micro and macro coevolutionary processes co-occur in the same individual plant, posing the question whether we should talk about plant coevolutions. In this review article, I begin by briefly discussing the framework of coevolution theory and explore the complexities of studying coevolution in natural conditions. Then I analyze the difference between plants, microbes and animal coevolution, by exploring the above- and below-ground behaviors.

Keywords: coevolution; local adaptation; Red Queen; arms-race; reciprocal transplant; plant defense

Introduction

Plants are subjected to continuous and various interactions with a multitude of animals, bacteria, fungi, and viruses, above- and below-ground. Biotic interactions are a fundamental driver of natural selection of genetic traits to maintain or increase the fitness and avoid extinction. Since Darwin's natural selection theory in *The Origin of Species*, coevolution was recognized as a force that drives the mutual adaptive evolution in interacting species (Darwin 1859; Wade 2007; Pazos & Valencia 2008; Kutschera & Briggs 2009). Theoretical studies of coevolution date back over 30 years (Thompson 1982), but still now few evidences have been reported that demonstrate the potential of coevolution in the species diversification.

Despite studies of ecologists that consider individuals of a population as genetically uniform in time, and studies of evolutionary geneticists that treat ecological adaptation without influences on the population mean fitness, coevolution is a dynamic process. Only recently, ecological studies on coevolution have begun to be considered as a transversal discipline (Wade 2007). Rapid accumulation of data on molecular and chemical ecology is providing new opportunities for studying plant–enemy coevolution.

Moreover, in simplified ecosystems like agricultural systems, the race between host–plant resistances and natural enemies imposes intense natural selection and often a rapid rate of enemy adaptation. The recent interest in the mechanisms underlying coevolution is owing to the need of managing devastating diseases. The aim of these studies is to develop long-time effective biocontrol practices against invasive

pests (Schroter et al. 2004; Burdon & Thrall 2008; Bousset & Chevre 2013).

The present review describes the framework of coevolution theory and explores the complexities of studying coevolution in the 'real world'. Moreover, it describes the evidence for coevolution in plant–insect and plant–micro-organism interactions by considering symbiotic, attractive, repelling, parasitic, and predatory behaviors. Finally, some suggestions on future directions to study coevolution in natural environment are provided.

Definition of coevolution

Coevolution implies a tight ecological interaction between two or more species. Coevolution is an evolutionary process that prompts the genetic adaptation of a species in response to the natural selection imposed by another interacting species and the effects might be reciprocal (Janzen 1980; Berenbaum & Zangerl 1998; Woolhouse et al. 2002). Coevolution can occur between any interacting populations: prey and predator, pathogen, competitor or mutualists. The selective pressures that each individual can exert on the other is expected to depend on the intimate nature and strength of the association (Hochberg et al. 2000; Thompson & Cunningham 2002).

The dissection of investigated coevolutionary relationships has shown the ecological ingredients necessary for plant–enemy coevolution. They can be summarized in three main points: (1) the natural enemy must have significant selective impacts on the host through a severe reduction of host-population fitness, (2) host-resistance diversity must impact on

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the evolution of enemy virulence, and (3) host and enemy populations must exhibit considerable genetic variability (Thrall et al. 2012).

The outcomes of coevolution depend on the combination of many features, such as genotypes of host and biotic enemy, whether the genome is haploid or diploid. The number of alleles involved, the dominance relationships between alleles, the number of loci involved and epistasis relationships, whether reproduction is sexual or asexual and the relative generation times of host and enemies are important determinants as well (Woolhouse et al. 2002). Moreover, theoretical models predict that in coevolution many outcomes are possible: stable polymorphisms, dynamic polymorphisms with cyclic or chaotic fluctuations in allele frequencies of varying amplitude and selective sweeps of favorable alleles (Woolhouse et al. 2002). In nature, however, the detection of coevolutionary processes is difficult. Therefore, most studies have focused on the detection of patterns of variation in genotypes or phenotypes that are consistent with either ongoing or past coevolution.

Theoretical framework and methods to test coevolution

In a natural environment, the selective pressure imposed by continuous interaction between host-plant and enemy involves constant fluctuations on allele frequency (Rausher 2001). Coevolution entails the rise of new alleles, by mutation or migration, and the fixing in the population (Woolhouse et al. 2002).

Two models have described the dynamics of the coevolution process. The first, the *Red Queen* hypothesis, is synthesized as ‘running as fast as you can to stay in the same place’. It posits that for a given species adaptation increases the fitness against another interacting species, but at the same time such adaptation of the first necessarily causes a decline in fitness of the second species (Figure 1a; Rausher 2001; Woolhouse et al. 2002; Paterson et al. 2010). Red Queen metaphor became central in the description of continuous race in the process of evolutionary

adaptation to prevent extinction (Antonovics et al. 2011; Jensen et al. 2012; Nemri et al. 2012). Such coevolutionary interactions give rise to continual natural selection for adaptation and counteradaptation in interacting species (Figure 1a).

The second evolutionary hypothesis of coevolution is known as the *Arms Race* model. Coevolutionary dynamics are described as a continuous escalation of defenses and counter-defenses gained with new genetic traits that can be fixed in the population through a slow process. In such a model, genetic improvements are accumulated in both populations (Figure 1b; Rausher 2001; Woolhouse et al. 2002). Failure to recognize the dynamic nature of the interaction could result in misinterpretation of the genetic basis of coevolution.

Temporal and spatial patterns

On an evolutionary scale, the natural selection of new genetic traits is a biological phenomenon. However, a few examples of studies on temporal patterns of coevolution examine through long-term field studies the evolution of host and enemy traits. The main experimental difficulty concerns the long-time scale, especially for hosts with long-generation times. For this reason, only a few experimental data are available on microbes and viruses interactions, due to the short micro-organism generation time (Buckling & Rainey 2002; Paterson et al. 2010).

Alternatively, phylogenetic methods are used to trace evolutionary histories of alleles implicated in host–enemy coevolution. This method is based on the idea that two interacting lineages will have completely congruent phylogenies if they have diversified exclusively by coevolutionary relationships (Cavender-Bares et al. 2009; Dinnage et al. 2012).

However, studies on spatial patterns are rather more common. This approach assumes that geographically separated subpopulations are at different stages of a coevolutionary process. The differential stages of local adaptation are an indirect proof of

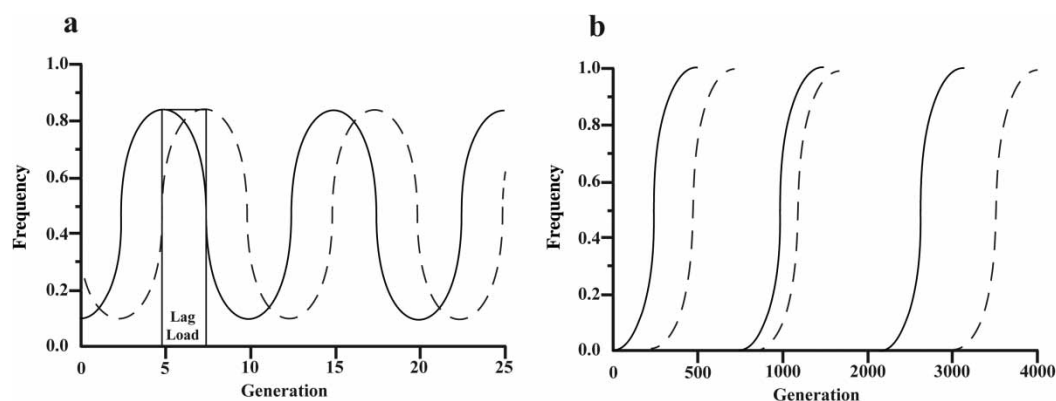


Figure 1. Allele frequency changes driven by coevolution. (a) *Red Queen* model: cycling of enemy (black line) and host (dashed line) allele frequencies as a result of frequency-dependent selection. The box shows the lag time between the cycles in host and enemy; (b) *Arms Race* model: a series of selective sweeps by host and enemy alleles derived by mutation are depicted.

occurring coevolution. The experimental model predicts that host–enemies that cohabit the same area (or sympatric species) are generally more adapted each other than species from geographically separated areas (allopatric species; Leimu & Fischer 2008; Bischoff & Tremulot 2011; Garrido et al. 2012). The test of local adaptation is nowadays the most diffused experimental approach to test coevolution in geographically isolated subpopulations.

Experimental approaches for local adaptation

The examination of local adaptation comprises: (1) the analysis of host-plant differentiation in phenotype and phenomenology; (2) the test in laboratory conditions of plant adaptation; and (3) the reciprocal transplant experiment to evaluate differences in fitness performances for both local and foreign species in the field (Kawecki & Ebert 2004; Laine 2007; Bischoff & Tremulot 2011). The assumption underlying this approach is that in their local site the host-plants should have higher rate of adaptation against local enemies than against foreign enemies of same species (Glynn and Herms 2004; Roslin et al. 2007; Toju & Fukatsu 2011; Kalske et al. 2012).

Transplant experiments have shown higher resistance in local adapted plants (Sork et al. 1993; Roslin et al. 2007; Cremieux et al. 2008), no differences in adaptation for local and non-local plant populations (Laine 2007), and even maladaptation (Cremieux et al. 2008; Hereford 2009; Kniskern et al. 2011; Bischoff & Tremulot 2011). Such reported coevolutionary interactions follow the Red Queen hypothesis: the continuous reciprocal pressure between plant evolution of genetic resistance traits and the rise of counterpart defenses in natural enemies. Under continuous evolutionary race, the mean population phenotype follows closely the adaptive changes of enemy population but with a lag time due to the time required by a plant population to respond to enemy new traits. The ‘lag load’ feature in the Red Queen model explains the presence of mixed stages in the local adaptation, as reported by experimental works (Figure 1a; Rausher 2001).

Empirical results on field with transplant experiments (Bischoff & Tremulot 2011) as well as meta-analyses on local plant adaptation (Leimu & Fischer 2008) confirm that local adaptation does not necessarily depend on geographical distances between plant populations; rather environmental differences, even a small spatial distance, may promote stronger local adaptation.

Despite the convincingly experimental data regarding the occurring local adaptation, the transplant experiment approach cannot dissect between the influence of abiotic and biotic aspect on local plant adaptation (Laine 2007). Stronger evidences regarding the reciprocal influences between abiotic and biotic factors on local adaptation of plants were exposed by Garrido et al. (2012). They examined local

adaptation in both *Datura stramonium* host-plants and their herbivore *Lema trilineata*, while controlling for the potential abiotic factors that mediate local adaptation. The data reported higher local adaptation of herbivore to host-plant than the host-plant adaptation to its herbivore (Bischoff & Tremulot 2011; Garrido et al. 2012). These data support complex evolutionary relationships; in fact, to herbivores the presence of host-plant and its resistance traits are the most significant elements in the environment, whereas plants must balance the evolution of resistance traits in response not only against multiple specialist and generalist herbivores but also against unfavorable abiotic factors and other biotic enemies.

Plant as host for coevolution

Proof of occurring coevolution requires evidence of genetic changes in the field for both host and enemy. Nowadays, it is a great interdisciplinary challenge to get experimental proofs of such condition. Hereafter a brief discussion regarding experimental evidences of coevolution in host-plants and animal and microbes enemies will be presented.

Plant–herbivore coevolution

Plant-feeding insects have engaged an evolutionary antagonistic interaction that led to the development of a variety of plant defense strategies to avoid extinction. Plant defenses can be classified into resistance against herbivore, tolerance to herbivore, phenological escape from herbivore and overcompensation (Agrawal 2000). Tolerance reduces the negative effect of herbivory on plant fitness, but the genetic bases of such adaptive strategy are less clear than direct resistance traits, though tolerance traits were subject to natural selection. Moreover, plant genotype and environmental conditions can influence the tolerance capacity of plants under attack. Tolerance is associated to faster growth and higher photosynthetic capacity than healthy plants (Agrawal 2000; Stowe et al. 2000). The general assumption is that tolerance and resistance are genetic alternative defense strategies. The rationale of such statement comes from the observation that plants with effective resistance traits limit the damaged area by deterring the enemies and do not need tolerance mechanisms to survive. Conversely, high-tolerant plants do not evolve strong resistance traits (Fineblum & Rausher 1995; Stowe et al. 2000). However, on field experiments show evolution of mixed resistance-tolerance strategies in *D. stramonium* in response to two chewing insects: the specialist *Lema daturaphila* and the generalist *Epitrix parvula* (Carmona & Fornoni 2013; Turley et al. 2013). These results confirm that generalist herbivores are more susceptible to plant secondary metabolites used as a resistance defense strategy, whereas specialists are less susceptible to resistance as a result of coevolution. In the last case,

tolerance is a more effective defense strategy for the plant. Moreover, in the case of contemporary attack from both enemies, that occurs often in nature, the plant response lies between resistance and tolerance and working as a complementary defense trait (Carmona & Fornoni 2013).

In the case of resistance in response to herbivory, more information is available on molecular and genetic mechanisms. Plants have evolved the capacity to perceive elicitor molecules after herbivore attack (Bonaventure et al. 2011; Maffei et al. 2012). Cellular transduction mechanisms fine tune the activation and regulation at local and systemic level of genetic activation of biochemical pathways for the biosynthesis of defensive compounds with different chemical nature and function (Maffei 2010; Mithoefer & Boland 2012).

Unlike generalist herbivores that are usually more susceptible than specialists to plant secondary metabolites, often specialist herbivorous insects develop different biochemical mechanisms to disable the toxicity of such direct defense compounds. In many cases, selective pressure have evolved detoxification mechanisms through enzymatic inactivation or by sequestration of toxic compounds (Nishida 2002; Després et al. 2007; Peng et al. 2007). Moreover, specialists can use the specific defensive chemicals as cue to locate the host-plants (phagostimulant function) (del Campo et al. 2001; Picaud et al. 2003; Bernays et al. 2004). The extreme example of coevolution is those herbivores that sequester the defensive chemicals and use them as a protective compound against predators and parasites and to attract mates (Cogni et al. 2012). The observed pattern of specialization reflects a consistent evolutionary relationship between host-plant and specialists (Becerra 2007; Bandeili & Muller 2010; Richards et al. 2010; Agrawal et al. 2012; Ali & Agrawal 2012).

Soil-dwelling enemies

Soil invertebrate herbivores comprise mainly insects and nematodes which feed on a wide range of plant species and produce significant economic loss in agriculture (Hunter 2001). While the above-ground herbivore–plant interactions are well investigated, less information is available on soil ecosystems because of the difficulty to study plant–herbivore trophic interactions below-ground.

Recent reviews have explored the chemical based recognition and selection of host-plants in soil-dwelling herbivores (Johnson & Nielsen 2012) and nematodes (Rasman et al. 2012). The underlined picture reveals a complex signaling network. To locate roots, insects and nematodes use general cues such as carbon dioxide, sugars, and glutamic acid. Moreover, specialized soil-dwelling herbivores may use the interplay between volatiles and soluble signals to locate host-plant roots, whereas plants may mask the respiratory emission of CO₂ and phagostimulant

signals (Johnson & Gregory 2006; Hiltbold et al. 2011; Johnson & Nielsen 2012; Schallhart et al. 2012).

Despite the increasing number of studies regarding the dynamics of root responses to soil-dwelling herbivores (Erb et al. 2012), few attempts have been made to understand the adaptive genetic mechanisms beyond root and root-feeders interactions. Even below-ground, in the similar way of above-ground, natural selection leads to the selection of genetic traits that cope the chemical defense strategies of plant hosts and take direct advance from induction of defensive secondary metabolites (Robert et al. 2012a, 2012b).

Despite the evidences from ecology studies regarding below-ground basic chemical interaction and trophic relationships (Rasman et al. 2005; Hiltbold & Turlings 2008), so far little information is available on the mutual influence of plant and soil invertebrate herbivores for the genetic selection of new traits.

Insect pollinators

The ecological interaction is expected to drive a convergent evolution between plant traits and pollen vectors. In the ‘pollinator syndrome’ model, plants specialize to their most effective pollinators and the level of plant adaptation to different pollinators is indicated by the reproductive efficacy of each pollinator (Aigner 2001; Fenster et al. 2004; Ollerton et al. 2009). The evolutionary hypothesis related to this theoretical model is that plants should evolve to increase specialization only for the pollinators that increase the fitness performances, as long as the gain from specialization is higher than the loss due by a lower association with other pollinators.

Studies have questioned the excessive simplicity of pollinator syndrome theory to explain the rise of floral novelty (Ollerton 1996). Many experimental observations point against the pollinator syndrome (Ivey et al. 2003; Sahli & Conner 2006; Gomez et al. 2007). Indeed, many taxonomically diverse pollinator insects visit a single flower species; moreover, the variety and abundance of pollinators often change on the base of seasons and pollination periods. Therefore, the predicted theoretical model is too simplistic for the explanation of genetic selection of traits in flower to attract specialized pollinators. Moreover, ploidy changes and genetic hybridization are more effective in generating a floral novelty than the pollinator syndrome (Ollerton 1996; Aigner 2001).

Different mathematical models suggest the presence of more profitable approaches to evaluate the effectiveness of pollinators in plant specialization. The proposed mathematical model moved beyond the simply ranking of pollinator by their effectiveness in plant phenotype toward the quantification of the trade-offs between plants and pollinators (Aigner 2001; Ollerton et al. 2009).

Experimental evidences for coevolution of plant–pollinator interaction have been provided by

multidisciplinary studies examining the distinctive phytochemical traits in phylogenetic related species and have tested the pollinator ability to dissect traits. The most effective plant traits for pollinator specialization have been underlined (Raguso et al. 2003; Reynolds et al. 2009). Floral emission of volatile organic compounds (VOCs) evolution is driven by pollinators and herbivores (Raguso et al. 2003). Moreover, the volatilome from two Australian orchid species, *Caladenia longicauda*, food deceptive, *C. arenicola*, sexually deceptive, and the F1 hybrids have been dissected. The experimental analysis correlated the distinct pollination strategy with the clearly chemical discrepancy in the VOC profile between the two species (Salzmann et al. 2006). However, from the insect pollinator standpoint, studies with the hawkmoth *Manduca sexta* have revealed a more complex ecological relationship. An odor-based associative learning mediates the interaction with flowers, along with innate preferences. The effect of such learning capacity in natural context remains poorly understood (Daly & Smith 2000; Riffell et al. 2013).

The continuous advances on molecular bases of pollination relationships will be useful instrumental to elucidate the rationale of reciprocal genetic influences between flower evolution and pollinator specialization.

Plant–microbe coevolution

Plants are constantly interacting with the microbes present in their environment. For host-plants, these interactions can range from beneficial (symbiosis) to detrimental (pathogenic).

Beneficial associations assist the host-plants in the assimilation of soil water and nutrients, mainly nitrogen and phosphate in exchange of carbon sources (Frohlich et al. 2012; Vafadar et al. 2013). The main plant symbioses are with mycorrhizal fungi and rhizobacteria. In both cases, the establishing of symbioses requires the recognition of specific chemical signals (Oldroyd & Downie, 2008; Parniske 2008; Oldroyd et al. 2009; Harrison 2012). Arbuscular mycorrhizal (AM) symbioses are the most ancient, over 400 million years, and are an excellent fossil record of host-plant–microbial interactions. The wide distribution of AM in all branches of plant phylogenetic trees suggests that symbioses might have been present in a common ancestor and perhaps were instrumental in the initial colonization of land (Brundrett 2002; Parniske 2008). In symbioses with AM fungi, many genetic components have been conserved in eudicots, monocots, and basal land plants (Delaux et al. 2013). The Glomales are the only monophyletic mycorrhizal fungal lineage that has coevolved with land plants throughout their history; other mycorrhizal fungi have polyphyletic lineages that represent parallel or convergent evolution. The coevolutionary plant-AM model shows an increasing level of commitment and specialization by plants and fungi, according to the *Arms Race* model

(Brundrett 2002). Moreover, the recent discovery of some genetic links between bacterial and fungal symbiosis led to the hypothesis that rhizobia root-nodule symbiosis evolved from mycorrhizal functions (Kistner & Parniske 2002; Parniske 2008; Oldroyd et al. 2009). However, the main reported proof of coevolution in plant symbioses come from studies performed by evolutionary biologists and few data are reported on genetic selection of new alleles that improve the fitness.

Plants and pathogens are involved in an intimate detrimental physiological and ecological interaction. The strength of the selective pressure depends on the virulence of pathogen, the driving force in host-parasite coevolution. Virulence is a specific product of plant–pathogen interaction; virulence does not depend on parasite or plant alone (Ebert & Hamilton 1996). The successful pathogen infection is determined by the combination of host and pathogen genotypes. A number of genetic models of infection have been proposed to investigate the reciprocal role in the infection (Agrawal & Lively 2002).

The traditional gene-for-gene model focus on the role of active host-resistance (*R*) gene products in response to the recognition of pathogen-produced elicitors or ‘nonself’ pathogen molecules known as avirulence (*Avr*) gene products (Agrawal & Lively 2002). The gene-for-gene model implies the possibility that coevolution is driven by selection pressure on pathogens to escape from the recognition by host *R* genes, and the reciprocal pressure on hosts to respond to novel pathogen traits (Dodds & Thrall 2009). However, genetic dynamics in plant–harmful pathogens interactions may be more complex than it is represented by the simple gene-for-gene model (Tellier & Brown 2008). Resistance to pathogens is often a polygenic trait (Burdon & Thrall 2009). Indeed, the major unanswered question regarding the evolution of plant–pathogen associations is the extent to which resistance and virulence depend on specific interactions between single genes (qualitative resistance) versus those in which resistance is determined by many genes, individually of minor effect (quantitative resistance) (Horger et al. 2012). However, the most widespread investigated resistance traits include quantitative resistance.

A diffused approach to detect coevolutionary influences between host and pathogen uses the transplant experiment, as described above. The occurrence of pathogen local adaptation is expected when: the pathogen is host-specific, it has a short generation time compared to the host and subpopulations are physically isolated. Usually, studies are performed on a geographical scale exceeding the maximum dispersal range of the interacting species (Niemi et al. 2006; Laine et al. 2011).

In situ and *ex situ* conserved genotypes comparisons have been used to ensure the local adaptation according to the mentioned elements. Qualitative and

quantitative differences in resistance traits of *Hordeum vulgare* attacked by the pathogen *Blumeria graminis* have been studied by comparing on field transplant experiments of *ex situ* conserved crop germplasm (in gene bank) and *in situ* conserved seeds (on farm). In *ex situ* germplasm, the increase of 'lag load', the time required by the host-population to respond to selection and the reduction of resistance due the absence of a continuous competition with evolving pathogens, was observed. Whereas, in *in situ* populations the increase of quantitative resistance traits was found. The results clearly endorse the Red Queen model of local adaptation. On the other hand, *ex situ* collection has showed the potential value to maintain old resistance alleles that can disappear in the *ex situ* population as result of disappearing of virulence loci in pathogen population (Jensen et al. 2012).

Recent advances on genetic base of resistance mechanisms allow to conduct targeted cross-year genetic studies on host-plant-pathogen association

(Kanzaki et al. 2012; Le Van et al. 2012; Horger et al. 2012; Thrall et al. 2012) to discover the intimate nature of genetic trade off.

Future of coevolution studies

Plants are immersed in a complex architecture of biotic and abiotic factors that occur at the same time. Natural selection pressure imposed on plants the fixing of new genetic traits that assure the best compromise of fitness in such a complex environment (Figure 2).

Since the basis of coevolution lie in the appearance and fixation of new genetic traits in the population, the identification of molecular bases of plant-enemy interaction is necessary to demonstrate the occurrence of coevolution. Often the genetic mechanisms of interactions have a polygenetic base, more complex than the simple gene-to-gene model for plant-pathogen interactions. Often the appearance of new traits should not be simply the effect of new

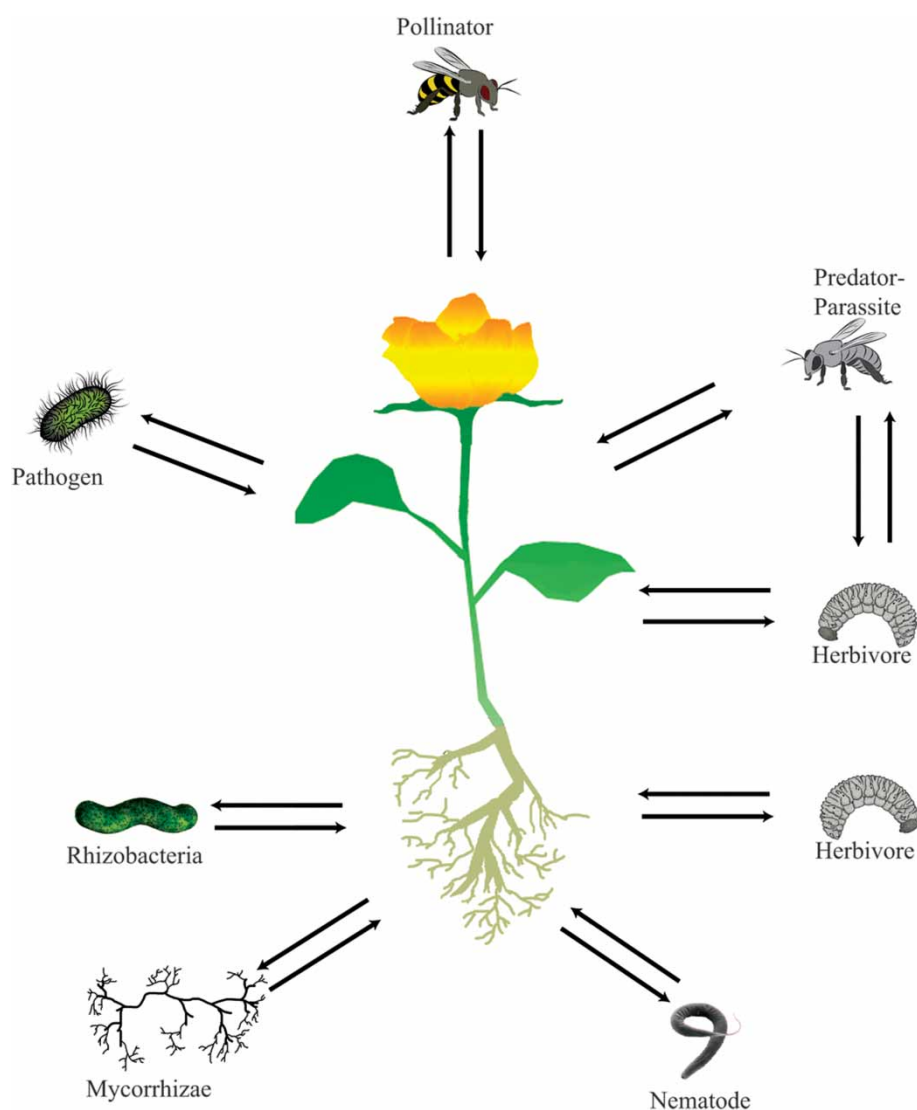


Figure 2. Evolutionary relationships between host-plant and biotic network. Biotic enemies and symbionts exert selective pressure on plant host, and the effects are reciprocal. However, plants must balance the evolutionary changes in response to unfavorable abiotic factors and other biotic enemies that occur at the same time.

alleles in existing loci. Progress in molecular biology needs to be exploited to elucidate genetic dynamics of coevolution.

Moreover, for the analysis of wild host–enemy interactions it is essential to link results from experimental systems to natural conditions. The restrictions of previous empirical studies on laboratory experiments, single populations or single time-points, have limited the possibility to draw considerable conclusions regarding coevolution in natural environments.

Studies on coevolution typically consider a single host-species interacting with a single species. In nature, plants experience a more tangled web of different enemies at the same time (Figure 2). The different enemy species interfere with the dynamics of others by multitrophic interactions between host-plant, plant enemy and enemies of enemy. Investigation of such complex ecological interactions would imply the transposition of described coevolution dynamics over the interaction between three or more genotypes. To understand the evolutionary paths of coevolution in natural environment, we need a reviewed theoretical framework to investigate the interplay between plant hosts, environment, and enemies.

In summary, progress in understanding coevolutionary dynamics in nature requires a deeper characterization of processes occurring at spatio-temporal scales, focusing more at the genetic level. One way to address these issues could be the development of new methods aimed to provide experimental evidence of coevolution, beyond the traditional phenomenological approaches; methods that focus wider on the elements that can influence the coevolution, integrating molecular-genetic approaches.

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